OBSERVATIONS UPON THE BIOLOGY, ECOLOGY AND LIFE HISTORY OF THE COMMON SHRIMP, PENAEUS SETIFERUS (LINNAEUS), ALONG THE SOUTH ATLANTIC AND GULF COASTS OF THE UNITED STATES

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In the United States, shrimp is by far the most valuable fishery resource of the States bordering on the South Atlantic and Gulf of Mexico, being exceeded in volume only by the menhaden which, however, it exceeds several times in value. This fishery is in fact one of the top-ranking fisheries of the United States and Alaska both in value and volume.

Although numerous species of shrimp are found along the South Atlantic and Gulf Coasts, only four are taken in quantities of commercial importance. The common shrimp, P. setiferus, is the most important commercial species, followed by the grooved shrimps, P. aztecus and P. duorarum, and the seabob, Xiphopeneus kroyeri, which is of least importance. All of these species belong to the family Penaeidae. The common shrimp is of major importance both on the South Atlantic and Gulf Coasts; the major fisheries for the grooved shrimp are in the Gulf of Mexico (although to a lesser extent on the South Atlantic also); and the seabob is utilized only in the Louisiana fishery, and there for drying purposes.

For a description of the development of the fishery, methods of fishing, facilities, geographical distributions, main fishing areas, and seasons, species entering the catch and catch statistics, refer to Anderson, Lindner and King, 1949.

The report to follow will touch upon the biology, ecology and life history of the common shrimp, Penaeus setiferus, along the South Atlantic and Gulf Coasts of the U.S. The material presented was extracted largely from Lindner and Anderson (1956). To a lesser extent material was obtained from published papers listed under 'References.'

No attempt will be made to justify the statements made as this has been done in the original papers.

Habitat

The common shrimp is most abundant in areas that are characterized by having an inland, brackish marsh connected by passes with an adjacent

shallow, off-shore area of relatively high salinity and mud or clay bottoms. The off-shore characteristics seem to be required by adults and perhaps also by the larvae, while the inland marshes appear to be required by the post-larval pre-adults. The adults are rarely found in abundance in the Gulf of Mexico in depths greater than 30 fathoms, and along the South Atlantic Coast the distribution appears limited to a narrow coastal belt not more than 8 to 10 miles off the coast and in less than 10 fathoms of water. The pre-adults inhabit brackish water and at times are found in water that is almost fresh.

Spawning

The females do not carry the eggs after fertilization takes place but deposit them directly into the water. The male attaches a spermatophore to the female some time prior to the emission of the eggs. Eggs are fertilized upon emission by the sperm contained in the spermatophore. A female will produce from 500,000 to 1,000,000 eggs in a single spawning, and it is probable that there is more than one spawning a season—at least for some females.

Most, if not all, spawning takes place at sea and not in the estuarine inland waters. It appears likely from available evidence that there is little difference between the spawning seasons in any of the localities studied along the South Atlantic and Gulf Coasts between South Carolina and Texas. There probably is not more than about 2 weeks' difference in the beginning of spawning between any of the localities. Spawning may start later and end earlier in some sections than it does in others, but in all of the localities it probably begins either during the latter part of March or early in April and may possibly continue into November, although it is practically completed by the end of September. There is evidence of two peaks of spawning success-one in April and May and the other toward the end of the spawning period. These appear associated with and probably caused by the habits of the shrimp and temperature.

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Larval development

The larval development of the common shrimp apparently covers at least ten distinct stages excluding the demersal spherical egg. These consist of five naupliar, three protozoeal and two mysis stages.

In brief, the larval development of P. setiferus requires from two to three weeks. Some twenty to twenty-four hours after the egg is spawned, the nauplius breaks the chorionic membrane and emerges. This minute organism (about 0.3 mm. in length) is to a great extent at the mercy of the prevailing currents, but is capable of some movement. During the next twenty-four to thirty-six hours the nauplius undergoes five successive molts to become a protozoea of approximately 1.0 mm. in length. It now has seven pairs of appendages, a pair of sessile compound eyes and a complete alimentary tract consisting of mouth, esophagus, stomach, intestine, and anus. Prior to this stage the food of the nauplius has been the yolk material carried over from the egg. This food supply is now exhausted, and henceforth the protozoea must capture its own food in order to survive. This transitional period is a critical one.

The third protozoea stage is followed by the first mysis which is about 3.5 mm. in length and possesses fourteen pairs of functional appendages and on the abdomen five pairs of buds which will soon become the pleopods. In the second mysis the pleopods are well developed, and rudimentary gills have made their appearance on the thoracic somites. With the succeeding molt the organism ends its larval phase and assumes the general proportions of a miniature adult. At the end of two post-larval stages and fifteen to twenty days after hatching, the young shrimp is only 5 to 6 mm. in length and is still planktonic. During this period of early development, the young shrimp have moved from the saline offshore spawning area to the brackish inside marshes, bays, and estuaries. Upon reaching these 'nursery grounds' they adopt for the first time, it is believed, a benthic existence.

The factors responsible for this inshore movement of larval shrimp have not been determined, but it is believed that for the young to reach the nursery grounds they must encounter favourable incoming currents. While capable of some movement, and perhaps responsive to a salinity gradient, they would certainly be quite helpless against outgoing currents. If spawning occurred at sea close to an inlet, the eggs could be swept through the passes on incoming currents, and the larvae reach the nursery grounds within a few hours.

Young shrimp

Young shrimp approximately 7 mm. in length are found during the spring and summer months in the

brackish areas which serve as their nursery ground for the next four to eight weeks of their existence. This habitat is a rich feeding ground with shallow water, muddy bottoms, rather widely fluctuating seasonal temperatures, and moderate to low salinity.

As the young grow, they move from the shallow waters of the marsh, bayou and lagoon into the deeper creeks, rivers and bays, making their first appearance on the inside fishing grounds when about 50 mm. long. The young first appear in the estuarine fishing grounds in June or July, depending upon the area, and by July or August they have begun to make their appearance in outside waters. Generally in the estuarine waters there is a gradient in size of the shrimp, smaller shrimp occurring in those waters farther inland and larger shrimp in those waters nearest the open ocean. This gradient in size appears more closely associated with locality than with salinity.

Growth

Growth data were obtained from shrimp marked in various areas of the fishery along the South Atlantic and Gulf Coasts of the U.S. The effective range of these data is from 100 mm. to 180 mm. From other sources the growth of shrimp smaller than 100 mm. has been estimated.

Growth is rapid during spring, summer and early fall, and negligible during winter. This suggests that the periods of rapid and slow growth are associated with temperature, and if this is so, we could expect them to vary somewhat from year to year and with locality. Our understanding of the growth is further complicated by the fact that shrimp of different sizes grow at different rates. The rapid growing season is from about March until the end of October.

We believe that shrimp reach about 80 mm. in length (from tip of rostrum to the end of telson) approximately two months after hatching. On this basis and applying the established growth rates an example of growth is: Spawning on May 1; young shrimp reached a length of approximately 80 mm. by July 1, 110 mm. by August 1, 130 mm. by September 1, 145 mm. by October 1, and 158 mm. by November 1. Growth from November 1 to March I would be negligible but if we assume that 2 mm. growth occurred during this period our shrimp would be about 160 mm. in length on March 1—the beginning of the spring rapid growing season. The shrimp would then reach a length of approximately 168 mm. by April 1 and about 173 mm. by May 1. It would be approximately 1 year old, mature and spawning during this spring season. Since the spawning season covers a period of 6 months or longer any number of combinations of growth are possible depending on the month spawned.

Migrations

Migrations were determined by tagging. The common shrimp has very definite patterns of movements but these vary in different areas.

We found that in one respect the movements of marked shrimp were similar in all localities studied on the South Atlantic and Gulf Coasts of the U.S. After the young shrimp first appeared on the inland fishing grounds they gradually worked their way towards the sea. This movement from inside waters to outside waters speeds up during two periods of the year—at the onset of winter and in the spring. These two periods seem to be associated with two groups of shrimp, the early-spawned group, and the later-spawned group.

Once the shrimp reach the outside waters their movements vary with size of shrimp, locality, and apparently also the time of the year. Small shrimp, 13 cm. or less in total length, did not undertake any extensive movements. Upon reaching the outside waters they remained there, almost immediately adjacent to their inland nursery grounds. The large shrimp, more than 13 cm. in total length, showed quite distinct behaviour patterns which varied with locality. These will be summarized on a geographical basis.

Atlantic Coast: Briefly our results indicate that most of the common shrimp of the Atlantic Coast, after migrating from inshore to offshore waters, do not move into very deep water far from the coast. Instead, they make seasonal migrations parallel to the shoreline, moving southward during the fall and early winter and northward in late winter and early spring. During late spring and summer, their movements are limited and random, so that they remain in the same general area. The larger specimens are much more prone to move considerable distances than are the smaller individuals. The longest known southward migration was performed by a shrimp released in North Carolina in October and recaptured 95 days later off the east coast of Florida—about 360 miles south of where it was released. The greatest northward migration was recorded for a specimen released in central Florida in January and recaptured 168 days later off the coast of South Carolina after it had gone about 260 miles.

Northern Gulf East of the Mississippi River: Tagging was limited to fall and winter months in the area between Mobile Bay, Alabama and the mouth of the Mississippi River. All that can be indicated at present about the movement of the shrimp in this region is that during the fall and winter they tend to move into deeper water and toward the mouth of the Mississippi River.

Northern Gulf West of the Mississippi River: In brief, along the Louisiana coast west of the Mississippi River the large shrimp moved offshore and scattered out during fall and winter. At all times they appear to be drifting about, like cattle on open range land. The only definite patterns were offshore and onshore movements, which evidently were associated with temperature changes and spawning, and a tendency to concentrate in certain areas, probably because of better feeding conditions. We believe the more or less aimless wanderings of the shrimp (but not the offshore and onshore movements) represent a search for food.

There appeared to be a natural barrier at the Mississippi River for we found neither east-west nor west-east crossings.

Central Texas: Results of tagging in this area are inconclusive due to distribution of the fishery when the marking was done. Indications are that shrimp from the central and southern part of Texas move south to the coast of Mexico during the fall and early winter, probably comparable to the movement along the South Atlantic Coast of the U.S. Likewise there is evidence of a springtime south-to-north migration from northern Mexican waters to Texas waters.

Longevity

Mortality of shrimp is apparently high and the number that live more than one year is small with respect to the total population and is probably not of great practical importance. Some shrimp live at least 16 months and possibly longer.

Temperature and salinity relations

While our temperature and salinity data are considered inadequate and are not as extensive as the biological observations, certain correlations are indicated in sections of the fishery where our most complete records are available. These observations may eventually be shown to apply to the entire fishery.

It appears that growth slows to practically nothing near the end of October when the water temperature drops to about 20°C and is resumed in the spring when the temperature again reaches approximately that value.

Spawning appears to be more closely associated with rising and falling temperatures than with absolute temperature. The comparatively abrupt rise in the spring temperatures coincides rather closely with the beginning of the spawning season and may, indeed, initiate it, while the season seems to terminate as soon as the temperatures begin to decline rapidly in the fall, even though they are at

that time appreciably higher than those which evidently induced spawning in the spring.

At first appraisal it would appear that there is little relationship between temperature and migrations. relationship between temperature and migrations. For example, in Louisiana, spring-spawned shrimp appear first in the trawl catches in inside waters in June, in outside waters adjacent to the coast in July, and offshore in August. This well-defined outward movement cannot be temperature-induced, since it occurs well before there is an appreciable drop in temperature. Judging from the behaviour of the shrimp during this period, we believe the offshore movement is primarily associated with the approach of adulthood and spawning. However, this offshore movement is later accelerated by falling temperatures. The phenomenon, evidently initiated by physiological changes in the organism itself, seems to be hastened and intensified during fall and winter by the external factor of declining temperatures.

Concomitant with the accelerated fall and winter offshore movement of the adults and sub-adults, the smaller, more immature shrimp move from the very shallow inland waters toward the Gulf of Mexico. These very small shrimp, which during summer are most abundant towards the heads of the bays are, during mid-winter, more abundant near the mouths of the bays and in the Gulf adjacent to the shore, where the temperatures are not so readily depressed.

A similar situation exists along the South Atlantic Coast. However, when the temperature begins to decline rapidly in the fall, the larger shrimp move southward along the coast rather than offshore as they do in Louisiana.

This change in habitat caused by winter temperatures can probably best be described as a general shift towards warmer waters, but with all sizes of shrimp still maintaining their size-locality separations.

Sudden, severe drops in temperatures in some localities will kill shrimp and in other localities will cause them to move offshore considerably beyond their normal range. It appears from the winter distributions of shrimp that the smaller shrimp are probably less susceptible to cold than are the larger ones.

The reaction of the shrimp to salinity is not clearcut. The young go to the inland areas of low salinity, and on approaching adulthood they move towards the more saline waters of the sea. It seems to us that the shrimp (at least the sub-adults) are rather insensitive to large fluctuations in salinity, but that they are quite sensitive to small changes in temperature.

In every locality, our trawl samples would almost always yield the smallest shrimp in the inside waters

farthest from the sea, and the largest in the outside waters. In general there was a progression in the size of trawl-caught shrimp, with the smallest ones in the waters of lowest salinity and the largest in the highest salinity. However, due to other complicating factors this apparent relation between size of shrimp and absolute salinity within relatively large ranges of salinity probably does not exist. The relation normally is between size and locality. That is, certain sizes of shrimp will be found in certain localities at certain seasons regardless of what the salinity may be (within relatively wide limits) at that particular locality and time. This does not mean, however, that there is no relation between size and salinity. Why is it that as the shrimp increase in size they head for the sea? We suspect this to be a reaction to salinity, related to spawning or maturity. We have observed that if the salinity becomes too low in an area, the shrimp will leave.

In winter there is a definite relation between size and temperature, with the largest shrimp seeking the warmest temperatures. This correlation does not exist during summer. In fact summer size-temperature relation is negative, but we can see no causeand-effective connection.

General

Perhaps the shrimp is its own worst enemy. Data from Louisiana (the area of greatest abundance) are suggestive of this. In spite of apparent continuous spawning throughout the entire season, evidently only the earliest and latest spawnings are really successful, and the latest spawning is concomitant with the earliest-spawned shrimp moving offshore from the inland nursery grounds. The second successful spawning in Louisiana (and the last in all other localities) does not seem to occur until vast numbers of shrimp have departed from the nursery grounds. Also in Louisiana, waves of oncoming young appear to be spaced about 2 months apart, which suggests spawning successes coinciding with mass departures of the preceding wave from the inner to the outer nursery areas.

Preliminary analysis of some of our data including that derived from tagging, suggests that the ratio between loss from natural mortality and gain in weight through the rapid growth of the individual animals is such that the total poundage of shrimp available to the fisherman would be increased if the shrimp were protected from the time they appear on the inside fishing grounds in summer until they move to outside waters in fall. Likewise, on this same basis, it might be advantageous to afford protection to the small shrimp while they are growing rapidly during early spring, or possibly to this same group during winter.

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It is rather widely accepted that in certain areas of its range (notably Louisiana) the shrimp is probably the most important animal both with respect to species-mass and food conservation. When we consider this point it is unfortunate that we do not know enough about shrimp to be able to predict with any assurance what will happen to the population when man does this or that. For example while we have suggested that it may be advisable to limit fishing of small shrimp, on the other hand, heavy exploitation of inside waters may result in a more extended spawning success owing to a reduced cannibalistic predation, with the obvious consequence of greater production.

We therefore arrive at the conclusion that well-controlled fishing experiments, together with additional research, are required before we can determine with any degree of accuracy how the shrimp population will respond to changes in fishing effort or in fishing seasons. Because the growth of the shrimp is so rapid, the experiments, if followed by competent observers and with adequate catch figures, need not be drastic in their approach. On the basis of our present information, experimental fishing of small shrimp during the periods when they are growing rapidly seems most promising.

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